Proofs of the Effects of Habitual Use in the Modification of Animal Organisms.

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Much has been written in regard to the supposed effects of use in inducing more or less permanent and inheritable alterations in the structure of animal forms. Darwin lays stress upon the effects of disuse in weakening the muscles which control the movements of the ears. He supposes, on the ground of disuse, that the drooping ears of the many domesticated races and species of mammals may have thus arisen. He also urges the same argument to account for the poorly developed and almost abortive eyes of moles and certain rodents. To decreased use he attributes the origin of the lighter wing-bones of domesticated races of ducks, while their relatively stronger leg-bones he attributes to increased use. He also supposes that the increased dimensions of the udders of cows and goats are partly to be attributed to the effects of unwonted and more prolonged use when bred from generation to generation for purposes of milking. He also cites approvingly the results of the experiments of Ranke, who showed that the flow of blood is greatly increased towards any part which is performing work, and again sinks or diminishes in amount when the part is at rest, concluding that, if the work is frequently recurrent, the vessels increase in size and the part is better nourished. From the frequent reference to the effects of use and disuse and his evident belief that such effects were inherited, it is clear that Mr. Darwin attached great importance to use and disuse as an agent in modifying species. In so far as Mr. Darwin appealed to the effects of use and disuse he followed the lead and accepted some of the conclusions of his great predecessor, Lamarck, who had published his own views more than fifty years before the appearance of the "Origin of Species."

Lately much activity has been manifested by the German biologists, under the leadership of Prof. Weismann, in testing the effects of the inheritance of mutilations in reference to the question of use and disuse. It is the opinion of the present writer that the method of experimentation resorted to by Weismann is altogether unsatisfactory, since the mutilations in the first place were made upon parts which were not only already rudimentary, but also after the ontogenetic processes had been practically completed. Weismann practiced the excision of the tails of mice in a series of successive generations without any inherited result, and forthwith concludes that mutilations are not inherited. This negative evidence, based on experiments in mutilating mice, is of absolutely no value whatever in solving the problem of the effects of use and disuse now before the present generation of biological investigators, as I hope to show

in the near future. One may be still more sweeping and even offer good reasons for the assertion that there is not now upon record a single instance of structural modification due to mutilation which has been even adequately traced or studied by the help of the rigorously exact ontogenetic method. Experiments in mutilating a few successive generations of mice are of no value in deciding this question, first, partly for the reasons already assigned, and, secondly, because there were not enough successive generations experimented upon, and, thirdly, because there is but little direct evidence to prove that structural alterations resulting through *external* mutilation are inherited. To hold up the results of such experiments as conclusive evidence against what are claimed to be the erroneous views and grounds of opinion of Lamarck and his followers may be regarded as scientific amongst Neo-Darwinists, but as a good old-fashioned Lamarckian such a proceeding appears to me just the reverse.

The evidence as to the effects of use in the modification of species was very meagre in Lamarck's time, and but little evidence of a conclusive character has been accumulated since, as is proved by the paucity of examples cited even by Darwin himself. Even the cases of the dung-beetles, where the tarsi of the anterior legs are completely lost in *Ateuchus*, the sacred beetle, the evidence that their absence is due to the inheritance of their very frequent loss through mutilation is uncertain. The only case where a mutilation seems to have been inherited is, as the writer first pointed out, that of the imperfect enamel crowns of the embryos of white rats studied by Von Brünn. In these cases the imperfection of the enamel coverings in the just erupting molars corresponded exactly to the enamel areas worn off through use at the tips of the crowns in the molars of the adults.

While it is impossible to subscribe to much that has been offered as explanatory of structural modification through use alone, there are many instances of structures the origin of which is to be accounted for in no other way. The crude hypothesis of Herbert Spencer ("Prin. Biology," ii, Chap. xv), as to the method of evolution of the vertebral column, while far better than the transcendental speculations of Owen respecting the general homologies of the vertebral bodies, with their appendages, can now be replaced with a far better one. While it remains true, as Spencer points out, that the segmentation of the vertebral axis is due, as even Rathke and Balfour recognized, to the mechanical requirements of such an axis and the conditions of growth under which it is placed, the details of this process have not even yet been fully worked out. In order to do so the vertebral axis of every distinct type must be critically investigated; the processes of the ontogeny of every one of its elements, no matter how minute, not simply its ontogeny, must be traced before comparisons and deductions are in order. Over a year ago the present writer took up anew the general subject of the vertebral column throughout the vertebrate series, with the result of finding that this structure is an example of continuous evolution as supposed by Herbert Spencer, in his article entitled

"*A Criticism on Prof. Owen's Theory of the Vertebrate Skeleton,*" and published in the *British and Foreign Medico-Chirurgical Review* for October, 1858. I find that it is possible on the basis of fact to completely substantiate, so far as the vertebral column is concerned, Mr. Spencer's conclusion, stated near the close of the article just cited, that: "It is a perfectly tenable supposition that all higher vertebrate forms have arisen by *the superposing of adaptations upon adaptations.*"

I find in fact that not only have the successively higher and higher types of vertebral elements grown out of one another in succession as the consequence of superimposition of new characters, but also that as a result of such superimpositions of new features a complex series of substitutions have resulted, which it is not in place to discuss in detail in this connection. It may be demonstrated that the growth and evolution of the jointed calcified vertebral column, after the development of the notochord was achieved and upon which the first expression of a segmented support was moulded, could take place in only one way, in forms with a free larval stage or such as developed quickly into an active organism, followed by a prolonged period of growth. It may also be proved that the only jointed calcified structure which could here satisfy the requirements of rapid, tridimensional, continuous growth in such a case without entailing inefficiency was the biconcave type of vertebræ, which are thus found to have a profound physiological and adaptive significance which has never hitherto been even dreamt of by the ordinary "*Ding an Sich*" school of morphologists, the offspring of the one-sided training now practiced in all European and American biological laboratories, in which the microscope, microtome and homologies, real or fancied, are the reigning fetishes. It may be shown also that the development of the vertebral bodies under such conditions is exogenous; that the mechanical conditions, definite motions and space relations of the parts involved are the determining factors in the evolution of a definitely-shaped succession of segments moulded upon a preëxisting notochordal rod. It may also be shown that, as layer after layer of new matter is superimposed upon the first trace of a vertebral body, these layers become successively wider and wider, and that the last formed or youngest and most external layers are the only ones which articulate by their edges and form the points of contact of the ends of the cylindrical vertebral bodies. It is thus easy to understand that, with every increment of growth, a new articulation is established between every two successive vertebræ, and that at the same time the innermost and first annular rings of calcified vertebral substance of successive vertebræ are pushed as much farther apart as the new rings at the periphery have grown in additional width. Thus arises that marvelously ingenious yet extremely simple form of calcified vertebral body which not only furnishes the means of continuous growth, but also that of continuous functional activity.

It may also be rendered certain that it is such a biconcave form of vertebral body which forms the basis out of which all the others have

grown. It may be shown that traces of the more primitive biconcave matrix of the vertebral body are embedded within the cartilaginous or even osseous matrix of the later stages as seen in some Batrachia and reptiles. It may also be shown that the epiphyses of the centra of higher types have their cartilaginous bases developed as ingrowing proliferations from the cartilage formed outside of the more primordial calcifying matrix which is broken or interrupted into a regular succession of recurring rings by the flexures of the body induced by the muscles during locomotion. This process of cartilaginous invasion begins to show itself in the very lowest of the true fishes or Lyrifera, viz., *Chimæra*.

There has been not even a partial abandonment of the primordial method of development of the vertebral bodies until we meet with forms which undergo a prolonged and complete development *in ovo* or *in utero*. There has, therefore, been no deviation from the primitive method of evolution of the calcified, flexible, jointed vertebral column until forms are reached in which specialization is so extreme as to require as an absolute physiological necessity an abbreviation of the processes of development of the column. Yet even in the most abbreviated form of development, as seen in Mammalia, including man, unmistakable traces are left over of the once biconcave condition of the vertebral segments. It may be shown that the physiological, histological, chemical, physical and mechanical conditions render the biconcave vertebral body the only one which is possible in the primitive condition; it therefore follows that there was no natural selection possible after the notochord was formed. There was only one groove, so to speak, along which the progressive evolution of the segmented, calcified, vertebral axis of vertebrates could proceed. There was no turning back once the notochord or vertebral matrix had been formed. The advent of the notochord "ordained the becoming," to borrow a phrase from Owen, of the future jointed column, and all the variations of the latter as manifested in species are the mere expressions of adaptive by-play. The same grounds are taken by Geddes in the discussion of the evolution of epigyny through perigyny and hypogyny in flowering plants.

Natural selection has therefore had absolutely nothing to do with the genesis of the primordial type from which all vertebral axes are evolved. At most the action of natural selection must be extremely indirect, and could in no way be operative except through the notochord, which may be shown to be a modified derivative of the intestinal wall of the same histological nature as the cellular axial cords of the tentacles of Hydrozoa and Scyphozoa. If it is possible to exclude natural selection it is also possible in a great measure to exclude the effects of inheritance. If it can be shown that the only thinkable or conceivable method of evolution of a jointed yet calcified and flexible vertebral axis is that actually realized, how is it possible to prove that inheritance even has anything to do with its development beyond providing for the ontogenetic recapitulation of its cellular matrix, the notochord and the arrangement of the muscles in a

series of lateral pairs, capable of effecting only one movement, which is itself the expression of an adjustment which it is impossible to prove first arose in any other way than as the result of obtaining the greatest physical effect in moving the body most efficiently through the water with only one kind of recurring and alternating muscular contractions happening on opposite sides of the body. Just here the natural selectionist jumps to his feet and declares, "There, you have granted all that we claim." But not so fast ; wait a moment. It is competent for him to first prove that this simple muscular training does not increase or stimulate the development of muscle through further histological and morphological differentiation and cell-multiplication, and the subsequent inheritance of this acquired complication and increased strength through use. Since there has not yet been offered an iota of conclusive evidence to the contrary, and, since the necessary investigations have not yet been made to disprove my position, I insist upon remaining an absolutely orthodox Lamarckian.

There are still other reasons for taking the above-stated position, which cannot now be referred to except briefly, as they arise from a consideration of the far more intricate and difficult question of sexuality. The greater part of the recent discussions of the significance and origin of sexuality are so transcendental in their character as to promise little of permanent value, since all of the hypotheses yet propounded, with the exception of the two radically different views propounded by Patrick Geddes and myself, overlook the importance and necessity of keeping in sight the general physical doctrine of the conservation of energy. No biologist has yet recognized with sufficient clearness the overwhelming importance of the principle of overnutrition, which was at once the cause of sexuality, the struggle for existence and the direct means of the evolution of all larval forms. Overnutrition, resulting in sexuality, was the means of heaping up potential physiological energy in the egg so as to render larval development and a larval struggle for existence a possibility ; and any other view of the origin of all or most larval types has little or no scientific warrant in fact. If, therefore, physiological energy was superimposed upon physiological energy or potentially stored, so to speak, in a germ-cell of exaggerated dimensions, it follows that the mainspring of evolution or its motive force is to be sought in sexuality and not in the Weismannian speculations as to the significance of one or two polar cells or the existence of a hypothetical germ-plasma which amounts in essence only to a restatement of the fact of heredity to which a hypothetical-physical basis is thus assigned. Since it can be proved that larval adaptations have occurred independently and wholly regardless of the attained differentiation of the parent, the fallacy of Weismann's doctrine of the immortality of the germ-plasma must be sufficiently obvious to those who have followed him in the development of his extraordinary errors.

I wish it to be distinctly understood that I do not consider all evolution as mechanical, but I do wish to be understood that the processes of evolution are physical and must ultimately be treated as physical problems.

To the elucidation of some of the grounds upon which hypotheses of mechanical evolution may be founded I have steadily devoted attention since 1877, in the belief, then, as now, that the only hope of the solution of many of the problems presented by the phenomena of adaptation lay in the direction sketched out in my first considerable essay, entitled, "On the Mechanical Genesis of Tooth Forms," published in the latter part of 1878. That essay met with no recognition amongst biologists except at the hands of my distinguished friend, Prof. Cope. In England, a deservedly well-known odontologist dismissed it, in a work on dental anatomy, with a characteristic British sneer and with comments that showed that he had not only not read it, but that he had also utterly failed to understand the grounds upon which my speculations were based. That line of odontological study has since been most profitably followed out in much greater detail by Profs. Cope and Osborn, but there are other and more definite proofs needed. Since the hard parts of animals are moulded by the soft parts, and not *vice versa*, what is now required is some evidence in the first place that hard parts do in reality suffer modification, through the influence of the actions of an animal, and that Lamarck's theory of use proves true, as happens in the case of several thousand species of fishes now living, notwithstanding the objections so glibly urged offhand by biologists whose special studies unfit them to express an opinion upon this subject.

The cases usually appealed to to prove the modifying effects of use are too complex, and the history of their parts is not always well enough known to afford conclusive evidence. In the series of cases now to be presented this is not the case. The entire history of the parts, directly affected by an exceedingly simple mode of use, is known from their earliest appearance until the completion of growth. The embryological, morphological and physiological sides of the question are therefore adequately represented in a simple case, and all that remains is to trace the kinetic side of the subject, or that involving the expenditure of energy, in order to complete the physical survey of the problem.

I have been aware for upwards of ten years that it is probable that the numerous transverse fractures in the so-called jointed or "soft rays" of fishes had probably arisen as the result of the interaction of the living fish and its surroundings. Only within a very recent period, however, has it been possible for me to find evidence, which I believe to be incontrovertible, in proof of such a conclusion. This evidence serves to demonstrate conclusively that Nature may and does make truly morphogenetic experiments if we will but pursue her clews until she is literally taken in the act of creating new features. As far as I am aware, the case about to be described is the first one that has been recorded that serves as direct proof of the doctrine that the structure of an organism may be altered by the actions of the organism itself.

The proof that the "soft rays" of fishes are normally fractured and more or less completely segmented by the resultant interaction between

the fins when in functional use, and the resistance offered by the surrounding water in which the animal swims, is based upon a single series of facts observed in the tails of young trout from a little less than, to somewhat more than an inch in length. In young trout that have just completed the absorption of their yelk sacks, it is found that the outer rays of the caudal fin are segmented in a direction different from that observed in the median rays, as shown in Fig. 1. This figure shows that the outer or extreme dorsal and ventral rays are fractured obliquely, while the median rays are broken or fractured in an exactly transverse direction. The obliquity of the fractures of the extreme dorsal rays is also exactly the reverse of those of the extreme ventral rays, so that the lines of fracture lie approximately parallel to an imaginary vertical line drawn up and down over the side of the whole fin.

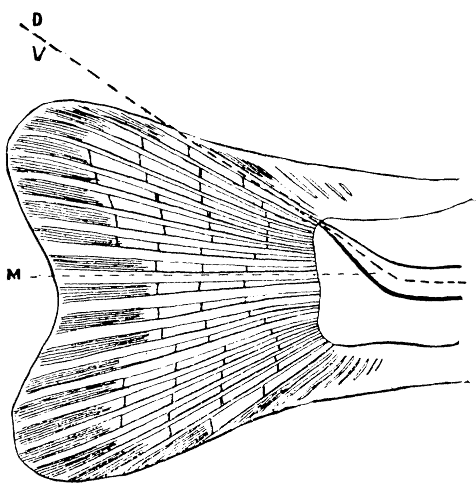

FIG. 1.

Now, what is the significance of these facts? In the first place, that the fractures are real physical breaks which are caused as the consequences of overcoming resistance is shown by the ragged, bruised appearance of the broken ends of the segments, and by the appearance of new breaks between those first formed as the fin-rays become longer and stronger, as the fish grows in size, until as many as two hundred or more may be formed in the course of each of the lateral halves of a single ray. Obviously, the only movements which are effective in bringing the tail into use as an organ of propulsion, are the vibratory movements from side to side, with which every one is familiar who has ever seen a fish swim. In so using the tail the resistance offered by the water is that which must be

offered to a flat vertical membrane supported by rays diverging radially from the hypural bones or cartilages below the upturned urostyle or notochord. Motion is mainly imparted to the caudal fin by the muscles of the urosome, or by that part of the tail of the fish intervening between the base of the caudal fin and the anus. The motion of the caudal fin is therefore controlled by the posterior part of the vertebral column and the lateral muscles of the urosome, and not through the morphological axis represented by a dotted line deflected upward and terminating between the letters D and V, so that the mechanical axis, or the axis which controls the movements of the whole fin, passes out far below the latter along the dotted line ending at M. The consequences are obvious; the resistance offered by the water to the motion of such an osseous framework of diverging rays is such as to break the median ones square across and those slightly below or above the mechanical axis in a slightly oblique direction, while the long rays at the extreme dorsal and ventral margins of the fin are actually broken across at an angle of nearly 45° with their own axis. If any other valid interpretation of the origin of the differences in the direction of the fractures or joints of the fin-rays of the caudal fin can be proposed, I should be glad to hear of them. But it is inconceivable that any other can be true.

While what is regarded as conclusive proof of the modification of hard parts, conformably to the operation of purely physical agencies has been offered above, it still remains to prove that the forms of soft parts are so modified. That this may be done is already evident from the data in my possession in regard to the modifications entailed upon larval stages which undergo specialized modes of development in the egg or reproductive passages of the female parent. If it can be shown that larval stages are structurally modified by physical agencies, it is tantamount to certain that the adult is not exempt from the influence of such agencies. Consequently the old debate as to the effect of use and disuse, and the interpretation of adaptations and inheritance on the basis laid down by Lamarck just eighty years ago, has not yet been disposed of, nor will it be by the fundamentally erroneous methods now almost universally employed by those biological investigators who take the opposite grounds.

In Fig. 2, the heavy curved or wavy lines drawn across the outline of the caudal fin show that the breaks, while practically conforming to a direction parallel to an ideal vertical line drawn across the whole fin, the individual breaks of the separate adjacent rays change position slightly with respect to such a vertical. If lines are now drawn through the transverse rows of breaks of the successive rays we obtain three lines symmetrically related to the mechanical axis of the fin. Three of these lines correspond to the three complete transverse lines of breaks or fractures, while the fourth is not yet complete, but enough of it is shown to prove that when complete it will conform to those in front of it. These major curved lines to which the lines of fracture of all the caudal rays conform, also themselves conform approximately to the outlines of the pro-

files of the successive myotomes, or lateral or muscular segments of the urosome when viewed from the side. These further correspondences and curves are not insignificant. They are undoubtedly to be traced to the

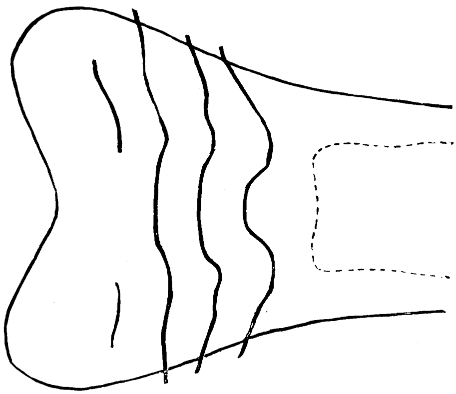

FIG. 2.

properties of strength at different points of the material fractured and the way in which the energy of motion exhibited by the myotomes of the lateral muscles of the tail is exerted upon rays lying at different levels in the caudal fin.

It may be stated that these figures are from actual camera drawings of the objects themselves, and that no liberties whatever have been taken in recording the facts, as permanent preparations in my possession will testify.

A study of the other fins of young fishes discloses the fact that the soft rays in the dorsal, anal, pectorals and ventrals are fractured in conformity with the exigencies of use. A study of the types of orders shows that wherever the "soft rays" occur their transverse fractures are due to the same cause; sometimes even pseudo-arthrodial articulations may thus result. The final conclusion is that the fractures of the "soft rays" of the fins of some six thousand species of fishes now living are the direct results of use. Disuse of the fins would result in absolutely depriving all this host of forms of one of their most salient characters. Whether the effects thus mechanically produced anew in the course of the life of every generation are inherited, is a matter of no consequence, since there is no need in this case for an appeal to the influence of heredity.